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Research article

Morphological appearance and effects of castration on blackback gorillas *Gorilla gorilla gorilla* in the EAZA ex-situ population

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Abstract

Currently, the sex ratio of the western gorilla *Gorilla gorilla gorilla* ex-situ population shows a tendency to balance due to an increase in the number of males. The gorilla's social structure is the harem (one male and two or three females) and this increase, together with a lack of space and/or facilities to accommodate new families in zoos, makes it impossible for many males to become breeding males leading a group. This excess of males needs to be managed. Different strategies have intended to alleviate this problem, such as forming bachelor groups or housing solitary males, but they have proven to be insufficient so castration has been considered. Castration could affect the development of these males who could be perceived as non-competitors by the silverback, therefore increasing his tolerance towards them and their acceptance in his family group. However, castration may produce side effects affecting the health of individuals, so that long term monitoring of castrated males is necessary. This study assesses the morphological development of some castrated and intact blackback males. Weight growth curves were elaborated for castrated and intact males and females of similar ages. Several morphometric measurements of both types of males were compared. Morphological measures are not significantly different between castrated and intact males. The average weight of castrated males is lower than that of intact males and similar to that of females, although weight growth curves show clear differences among the three groups. Castrated males showed none of the secondary sexual traits that are present in intact blackbacks. Overall, castration upon reaching the blackback life-history class promoted a lower average weight and a lack of sagittal ridge development but similar body growth to intact males.

Introduction

The European Association of Zoos and Aquaria (EAZA) was created in 1992, with the main objective of facilitating cooperation among European zoos and aquariums in order to contribute to the conservation of species by keeping ex-situ populations while ensuring their well-being and sustainability, in order to promote conservation, education and awareness and to contribute to scientific research.

EAZA Ex-situ Programmes (EEPs) are developed for the most vulnerable species on the planet. These programmes regulate captive breeding by promoting best management practices and, through studbooks, they collect information on the status of each individual of the population. Demographic and genetic analyses are performed from these data, allowing optimisation of population management. EEPs are coordinated by means of Regional Collection Plans (EAZA 2019).

Gorillas *Gorilla gorilla gorilla* are managed through an EEP in EAZA institutions. This is a Critically Endangered species (IUCN 2021). The main objectives of the EEP for gorillas are to promote ex-situ and in-situ conservation by maintaining a healthy and sustainable ex-situ population, promoting research to increase the knowledge on this species and collaborating with in-situ conservation projects (EAZA 2019).

The EEP gorilla groups are mainly formed by a silverback—the breeding male—and several breeding females with their offspring according to a harem social system, which is the norm for gorillas in their natural habitat (Abelló et al. 2017a, Magliocca et al. 1999). However, due to the balanced birth sex ratio of recent decades, a certain number of males will never get the chance to lead a harem group. In the wild, males that leave the family group at the onset of sexual maturity may associate with other males, thus forming bachelor groups as a transitional stage (Gatti et al. 2004). Males can also be found wandering alone in search of females to form their own reproductive group (Magliocca et al. 1999, Watts 1991, Yamagiwa 1986).

Since the 1980s, the number of males in zoos has increased due to a balanced sex ratio and the longer life expectancy that males have in captivity. Therefore, some males will never get the chance to lead a breeding group after reaching sexual maturity (Vermeer et al. 2014). This is the so-called 'surplus males problem'.

In order to deal with this situation, some measures have been implemented by the Gorilla EEP when managing the population: a) To place only two or three breeding females per group, which allows the formation of more breeding groups; b) To keep young males, that will become new breeding males in the future, in their family groups longer (to about 12 years old) only if no serious incompatibility occurs; c) To reduce the breeding rate by enlarging the interbirth period with the use of selective contraception, allowing reasonable population growth; d) In exceptional circumstances, to house some of the older males alone, when the company of a conspecific would seriously decrease the welfare of these individuals and e) To promote the formation of bachelor groups, as a transitory stage before joining a breeding group in some cases, and as a definitive state in other cases. Some males in the bachelor group, when fully grown, become aggressive towards the other males and need to be relocated. They can replace a breeding male if such a possibility exists but, if not, they will probably have to be kept alone. Other alternatives have been sought to overcome these problems such as castration of young males and assisted reproduction techniques with sex selection. The latter is not yet developed but would be a very valuable tool to allow sex ratio modification (Abelló et al. 2017a, Vermeer et al. 2014).

During the first three years, gorillas are considered infants, at age four to six they are considered juveniles, and after that age they are considered sub-adults. Females become adults at 8 years although the first pregnancy usually takes place later, when about 12. In captivity there are some records showing pregnancy at 6 years old. Males are usually called blackbacks between 10 and 12 years old, young silverbacks between 13 and 15 years, and fully matured and grown from 15 years when they are known as silverbacks. When males reach the blackback period, and sometimes before that age, they have to leave the group in order to live alone, in a bachelor group, or with some females. During this period, from blackback to silverback, males grow in size and stature and the reproductive system fully matures, together with the appearance of secondary sexual characteristics such as the development of the silver saddle of hair on the back and legs.

The first male castration in the Gorilla EEP was done in 1990. Wim Mager (Apenheul Zoo), foreseeing the problem of an excess of gorilla males, decided to castrate an infant male gorilla to monitor and evaluate whether his development was adequate and whether he could stay in a family group without suffering aggressions from the silverback and other members of the group. The castrated male developed a body size similar to that of a large female and did not develop silver hair on his back and legs, nor secondary sexual characteristics. He went through two harem groups during his lifetime and he never received any serious aggression; on the contrary, he showed a high degree of socialisation. This male died at the age of 22 from causes unrelated to the castration procedure (Vermeer et al. 2014).

Considering this experience, between 2007 and 2018, the Gorilla EEP decided to castrate 12 infant gorilla males under 4 years old and monitor their development to confirm whether this measure could be a new management tool for males that could not be assigned as breeding males to a harem group. This could be a way to provide them with a better life, by keeping them in a conspecific social environment without suffering aggressions from the silverback in the case of a harem group, or from other males in a bachelor group, when reaching sexual maturity. When selecting males that could be castrated, genetic value was taken into consideration in order to help maintain genetic diversity in the Gorilla EEP population.

Monitoring the development of the castrated gorillas was a first concern and ethological research was carried out during 2014–2017 (Létang et al. 2021). Results clearly show that castrated gorillas display a high degree of social behaviour and that there is a high tolerance towards them from the other individuals of the group, including the silverback (Létang et al. 2017, 2021).

A detailed literature review revealed information on castration effects in different animal species, including some species of primates but not gorillas, and in humans. These effects include anaemia in dogs (Sundburg et al. 2016), increased heart problems and diabetes in rats (Ayaz et al. 2015), osteoporosis or bone disorders in rhesus monkeys (Kessler et al. 2016), skin changes and absence of secondary sexual characteristics in humans (Licea and Castelo 2006) and a decrease in sexual behaviour in dogs and cats (McKenzie 2010). Furthermore, in humans, dogs and cats it has been observed that castrated individuals show a tendency to gain weight (Edney and Smith 1986, Licea and Castelo 2006, McGreevy et al. 2005, Sanborn 2007, Spain et al. 2004, Stubbs et al. 1996).

There are also some potential positive effects such as the reduction of aggressive behaviour in hamadryas baboons (Koot et al. 2016), a decrease of tumour production in dogs and cats (McKenzie 2010, Sanborn 2007) and an increase in life expectancy in rhesus macaques and humans (Maklakov and Lummaa 2013, Wang et al. 2016).

This study evaluates the morphological effects on male gorillas of castration at their blackback life-history stage (between 10 and 12 years old, Magliocca et al. 1999), considering that major changes in development will occur in the juvenile and sub-adult phases. For this purpose, weight increase in castrated and intact males as well as in females was compared during development until the age of 14. Body, arm, forearm and leg length were also compared between castrated and intact males.

Materials and Methods

To study how castration can affect the somatic development of male gorillas, the evolution of weight and some morphological measures were taken into account, comparing them with both intact male and female individuals. In addition, the degree of development of secondary sexual characteristics was assessed.

Weight

The information on the weights of gorillas at different ages was obtained from the data registered in Zoological Information Management Software (ZIMS, https://zims.species360.org), an international programme where many zoos enter information of the specimens from the different species they keep. Weights are usually taken opportunistically when veterinary interventions are required. In some zoos, there is a scale strategically placed on the daily pathway or inside the gorillas' rooms that allows more frequent weighing. Overall, there were 126 records from 1967 to 2019 (11 castrated males between 2007 and 2016, 48 intact males and 67 females) in 16 European zoos. Since gestation lasts for 255 days on average (Abelló et al. 2017b), weights recorded 6 months before and 4 months after the date of parturition were excluded. Finally, only those individuals for which there were more than 10 weight measurements (6 castrated males, 22 intact males and 36 females, from 13 European zoos) were included (Table 1). The mean number of years (±standard deviation) for which weight records were available was 7.61±4.0. The mean percentage of years (±standard deviation) for which there is a measure of weight

Table 1. Number of gorillas (intact and castrated males and females) from which weight records have been obtained according to the institution where they are located. Column A indicates those with more than 10 weight measurements (Figure 1). Column B indicates those with more than 10 weight measurements and an age equal to or less than 14 years (Table 4). Column C indicates those with morphometric measurements (Table 5).

Zoo	Number of gorillas							
	Males						Females	
	Intact			Castrated				
	A	B	C	A	B	C	A	B
Amnéville Zoo (France)	5	5	0	-	-	-	-	-
Artis Zoo (Holland)	-	-	-	-	-	-	1	1
Barcelona Zoo (Spain)	-	-	-	-	-	-	3	3
Beauval Zoo (France)	7	7	3	2	2	1	6	5
Belfast Zoo (Northern Ireland)	-	-	-	-	-	-	2	2
Bristol Zoo (England)	1	0	0	-	-	-	5	5
Burger's Zoo (Holland)	--	-	-	-	-	-	1	1
Chessington World of Adventures (England)	1	1	0	2	2	0	-	-
GaiaZOO (Holland)	2	2	0	2	2	2	5	3
Givskud Zoo (Denmark)	-	-	-	-	-	-	1	1
Howletts Wild Animal Trust (England)	5	5	0	-	-	-	11	9
La Vallée Des Singes (France)	-	-	-	0	0	1	-	-
Parque de Cabárceno	1	0	0	-	-	-	1	0

with respect to the age of the gorilla is 54.39±28.35 for castrated males, 53.48±26.25 for intact males and 55.21±27.58 for females.

Morphometric measures

The zoos that keep gorilla populations were asked to take several photographs of each individual when they were near an element of the facility with known measurements in two directions of space (vertical steel mesh or window frames) and which would serve as a scale. Morphometric measurements of the animals are indicated in Table 2 and Figure 1 and were calculated using photogrammetric techniques on these photographs.

The error resulting from the distance between the scale and the anatomical element to be measured (i.e. arm or leg) was assessed in the laboratory using photographs in which the distance between the object of known length to be measured and the scale was set at 0, 10, 20, 30, 40 and 50 cm. At each distance, the photo was taken

Table 2. Definition of morphometric measurements.

Measure	Definition
Body length	From the end of the neck to the lower back of the gorilla
Arm length	From the beginning of the shoulder to the elbow
Forearm length	From the elbow to the wrist
Leg length 1	From the upper part of the waist to the knee
Leg length 2	From the knee to the ankle

Figure 1. Morphological point references used for the morphometric measurements. Blue: sagittal crest, yellow: body length, red: arm length, pink: forearm length, green: leg length 1, orange: leg length 2.

five times. The percentage error between the actual measurement of the object and that obtained from the photograph was calculated according to Galbany et al. (2017). A generalised linear model with distance as the covariate and the error percentage as the dependent variable shows a highly significant association ($F_{1,7}$=107.47, P<0.001), so that the error increases by 2.1% for every 10 cm distance (β=0.21, t_7=10.37, P<0.001). Therefore, the accuracy decreases as the distance increases. At a 30 cm distance, the error percentage was 6.18% (95% confidence intervals, 5.04–7.35%), a margin of error broadly similar to that reported for a range of primate morphology studies (e.g. Bailey 2004, Galbany et al. 2005, 2016). Therefore, only those photos where the distance between the gorilla and the measurement scale did not exceed 30 cm were used. To reduce other sources of error, the photos were chosen following two criteria: a) the anatomical element to be measured had to be found in the same plane of space as the element used as a scale and b) the gorilla should be found in the centre of the image and in a sitting or standing still position. Trigonometric functions were used when necessary (Figure S1).

All measurements were taken in centimetres by the same observer (CMT) and the morphometric measurements were repeated five times for each gorilla in each photograph in order to assess precision (intra-observer error). The mean intra-observer coefficient of variation for all the measurements taken was 0.036 cm (range: 0.02–0.05 cm).

All measurements were conducted using the ‘measure tool’ in ImageJ v1.47 (Abramoff et al. 2004); measurements were collected with single pixel resolution using a mouse to identify scale as the line in ImageJ.

Finally, morphometric measurements were obtained for three intact and four castrated males with ages between 10 and 15 years. Given that measurements have been taken in the same way for both types of male, their comparison allows evaluation of whether castration has affected the growth of these morphometric elements. The presence or absence of a sagittal crest was also reported (dichotomous variable). In this case, the animals used were the three previously mentioned intact gorillas and five castrated gorillas.

Statistical analysis

The initial exploration of the data showed that weight variability increases with age, so the square root of weight transformation has been used to avoid heteroscedasticity. Generalised additive mixed models (GAMMs, Zuur et al. 2014) were used to estimate trends in weight growth curves in intact and castrated males, and in females. These models incorporate smooth functions of one or more covariates and are thus able to model non-linear relationships between covariates and the response (Rose et al. 2012). In this way, they achieve more realistic adjustments to growth curves than those that adjust a predetermined sigmoidal growth based on a few parameters: asymptotic value, maximum growth rate and age at maximum growth rate (Giraldo-Deck et al. 2020). GAMMs were fitted to each weight growth curve, considering age as a covariate with a non-linear effect on the square root of weight (response variable). Repeated measures on different individuals as well as their zoo of origin were controlled for by including two nested random factors (gorilla factor nested in zoo factor). Finally, a normal distribution of errors and the identity as link function was assumed.

The age of castrated males did not exceed 14 years, so for the comparison of growth curves between classes, the analyses for intact males and the females have been restricted to this growth period. The comparison of weight growth curves was carried out with a similar GAMM but to which a fixed factor ‘condition’, with three levels (intact and castrated males and females), and the interaction with the non-linear effect have been incorporated. Post hoc comparison of the interaction was carried out following Rose et al. (2012). The models were validated by verifying the normality (QQ plot) and the homogeneity of variances (residual plot versus adjusted values) of the residuals. The Mann-Whitney U test and the Bonferroni correction were applied to test the hypothesis of the interval morphometric variables. The presence of a sagittal crest was analysed with Fisher’s exact test. The analysis was performed with R 3.5.2 (R Core Team 2019).

Table 3. Results of the analysis of generalised additive mixed models (GAMMs) showing the non-linear effect of age on weight development of females, and intact and castrated males. edf: effective degrees of freedom of the non-linear effect; df: degrees of freedom; R2: percentage of variation explained by the model.

Factors	Levels	edf	F	P	R^2
Fixed	Female	8.93	2236	<0.001	92.0
	Intact male	8.91	3581	<0.001	94.0
	Castrated male	8.61	1328	<0.001	92.0

Results

Weight

The GAMMs show a significant non-linear effect of age on weight for each of the three growth curves (intact and castrated males, and females) explaining over 90% of deviance (Table 3). Considering that the effective degrees of freedom (edf, Table 3) are calibration values that determine the shape of the curve, they indicate a strongly non-linear pattern. In the case of intact males, the growth rate increases until approximately 20 years of age, reaching a weight close to 225 kg. From this age, there is a process of weight reduction towards 175 kg in 35-year old gorillas (Figure 2). In the case of females, this continuous growth rate occurs until they are 12 years old, reaching a weight of 100 kg. From this age, weight oscillates until the age of 30, when it begins to decrease towards 75 kg in older females (40 years old, Figure 2). In castrated males, the growth rate is similar to that of females, reaching a weight of 100 kg at 10 years of age. From here on and for the remaining four years of data, weight stabilisation is observed (Figure 2). Although there is no further information for castrated males, their curve characteristics are more similar to those of females than to those of intact males (Figure 2).

The mean weight (±standard deviation) up to 14 years of age of castrated males (107.47±4.19 kg) does not differ from that of females (107.2±7.94 kg) although it does so from that of intact males at that age (190.88±4.19 kg, Table 4A). However, the weight growth curve up to 14 years of age of castrated males is significantly different from the growth curves calculated for intact males and females (Table 4B).

Morphological measures

The four castrated males aged 10–15 years had smaller morphometric measurements than the three intact males aged 10–13 years, although the differences are not statistically significant (Table 5). There are marginally significant differences concerning the presence or absence of a sagittal crest; all castrated males except one lack the crest (Fisher`s exact test P=0.07, Figure S2).

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Figure 2. Weight development as a function of the age of intact (n=23) and castrated (n=6) males, and females (n=37). The curve is fitted from the command geoom_smooth (method='gam') from the ggplot2 package (Wickham 2016).

Discussion

This study focuses on how the early castration of male gorillas can influence the evolution of weight during growth as well as different parts of the body's anatomy, including some secondary sexual characteristics, during the first 14 years of life. In order to do this, these variables were compared between castrated males, intact males and females. The results show that there are some differences between the castrated and intact male gorillas and that castrated males are more morphologically similar to females. These differences could help to understand the results from behavioural research (Létang et al. 2021) that showed that silverbacks had better tolerance of castrated gorilla males and that those individuals had a higher social profile.

This study shows that the pattern of gorilla weight development in captivity is a function of the age of the individual; this explains more than 90% of the weight variability. While intact males sustain their development for at least 20 years, females do so for up to 12 years. The development of castrated males extends for up to 14 years although with a different curve shape, reaching weights similar to those achieved by females but well below those achieved by intact males at the same age. These differences are similar to those found by Vermeer et al. (2014). In castrated macaques *Macaca mulatta*, no weight differences have been observed at any vital stage (Richards et al. 2009), whereas in humans, dogs and cats castrated individuals show a tendency to gain weight (Edney and Smith 1986, Licea and Castelo 2006, McGreevy et al. 2005, Sanborn 2007, Spain et al. 2004, Stubbs et al. 1996). Consequently, it is highly probable that if castrated individuals do not follow a very strict diet, they would potentially gain weight in the future, thus possibly leading to other problems derived from being overweight, such as dyslipidaemia, insulin resistance and metabolic syndrome (Ayaz et al. 2015, Bays et al. 2013, Paniagua 2016).

Since the same procedure was used to take morphometric measurements in intact and castrated males, their comparison

Table 4. Comparison of the mean weight reached during growth up to 14 years of age for the three types of individuals (fixed factor condition). The estimates for intact males and females indicate the difference with respect to castrated males and the value corresponds to the square root of the mean weight calculated by the model up to 14 years of age. The ANOVA results are also displayed. df: degrees of freedom.

						ANOVA						
Factor	Levels	Estimate	SE	t	P	F	df	P	Levels	F	df	P
Fixed	Castrated male	6.61	0.28	23.64	<0.001	13.85	2	<0.001	Female - Castrated male	0.49	1	0.49
	Intact male	1.22	0.32	3.83	<0.001				Castrated - Intact male	22.76	1	<0.001
	Female	0.29	0.31	0.94	0.35				Intact male - Female	26.54	1	<0.001

Table 5. Median and quartiles (25%, 75%) of morphometric measurements (cm) of blackback gorillas between 10 and 14 years old. The values of the Mann-Whitney U test are shown, as well as the number of intact (n_1) and castrated (n_2) individuals. All tests are non-significant after applying the Bonferroni correction.

	Intact		Castrated					
	Median	Quartile (25%, 75%)	Median	Quartile (25%, 75%)	U	n_1	n_2	P
Body length	78.52	62.45, 96.10	57.14	51.49, 65.55	1	3	4	0.08
Arm length	44.51	39.78, 57.45	32.30	29.56, 36.96	0	3	4	0.03
Forearm length	34.87	31.87, 53.80	31.47	30.91, 32.92	2	3	4	0.16
Leg length 1	38.44	25.51, 38.72	25.72	25.08, 29.31	2	3	4	0.16
Leg length 2	31.70	26.61, 37.72	22.91	21.68, 26.49	3	3	4	0.29

is appropriate and does not show differences. In other words, while weight differences at 14 years are clear between intact and castrated males, castration did not seem to influence the growth of individuals, although the small sample size must be taken into account and more research with a wider database would be interesting. In addition, it must be noted that the males are still in the development phase. Since humans with hypogonadism may present an alteration in the proportion of limbs with respect to body length—usually longer than expected—and bone mass may not develop to normal levels (Nieschlag and Behre 1998), it is important to be aware that these potential alterations that could occur in castrated gorillas at later developmental stages. Muscle development could also be affected. In some primates, such as rhesus macaques, pigtailed macaques and baboons, the experimental administration of testosterone induced an increment of musculature, leading to the conclusion that, in these species, testosterone could be related to muscle development (Muller 2017). Taking these results as a reference, the castrated gorillas may have had a lower muscle mass than intact males due to a lack of androgens.

The sagittal crest develops in intact blackback individuals, whereas it developed in only one castrated blackback individual in this study. Given that in primates 95% of androgens are synthesised in the testis (Rommerts 1998), castration could cause a shortage of these hormones. This may explain the lack of secondary sexual characteristics (Owens and Short 1995), as observed for the first castrated gorilla in the 1990s (Vermeer et al. 2014). The tolerance and social interactions of castrated males between 3 and 11 years old is higher than for intact males (Létang et al. 2021). In consequence, the lack of androgens could be the cause of a more submissive behaviour from the castrated males towards the silverback and, at the same time, the lack of secondary sexual characteristics making them more similar to large females resulting in increased tolerance from the silverback towards them. Due to this higher tolerance, castrated gorilla males could remain in the family group, enjoying a social life and contributing to the social dynamics of the group.

Another characteristic of a silverback is his capacity to release a strong and characteristic smell when excited, which is related to the presence of androgens (Klailova and Lee 2014). It would be interesting to test for the lack of or decrease in the amount of odour released by castrated individuals, as this could also be related to the silverback's tolerance, as he would not recognise a castrated male as a potential competitor in the group.

It will be important to carry out a long-term physiological study of castrated individuals in order to assess whether they could present any physiological alteration that may affect their health. This could be assessed by haematological analysis, by performing opportunistic blood collection in case the animal is anaesthetised for any reason, or with a stool study (Takeshita et al. 2017).

Under the hypothesis that castration does not have any side effects on the health of these individuals, or causes only mild side effects, castration could be considered an alternative option for the management of excess males in the Gorilla EEP population. In this way, males with a lower genetic value that would not have the opportunity of becoming silverbacks in a breeding group throughout their lifespan could still enjoy a socially rich and active life in a group of conspecifics, without intense confrontations with the silverback.

In the future, if an efficient technique of assisted reproduction with sex selection is developed, the current sex ratio trend could be modified by selecting female embryos and avoiding an excess of males. In humans, these techniques have already been developed and in some primate species sperm can be selected by means of flow cytometry techniques based on the difference in DNA contingency between the X and Y chromosomes (O'Brien et al. 2002 cited in Abelló et al. 2017a).

Conclusions

Males show a different weight developmental pattern compared to females and in adulthood are double the weight of females. Castrated males show a developmental pattern at 14 years of age that is different from that of intact males and females, but the average weight is similar to that of females and well below that of intact males.

The body and extremity lengths of castrated males are shorter than those of intact individuals of the same age class, but this difference is not significant. However, there are indeed differences in terms of the weight reached, which could be a consequence of inferior muscle development.

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Ethical statement

This research project was designed in accordance with best practices and highest ethical standards, and meets national and international legislation requirements. Moreover, all methods comply with the EAZA Code of Ethics (www.eaza.net) and the WAZA Code of Ethics and Animal Welfare, namely the Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquaria (www.waza.org).

The authors declare that they have no conflicts of interest related to this work.

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References

Abelló M.T., Rietkerk F., Bemment N. (eds.) (2017a) E*AZA Best Practice Guidelines: Great Ape Taxon Advisory Group GORILLA (*Gorilla gorilla gorilla*). Second edition.* Barcelona, Spain: Barcelona Zoo. https://www.eaza.net/assets/Uploads/CCC/2017-BPG-Gorilla-approved.pdf

Abelló M.T., Felter Y., Glatston A., Holtkötter M., Redrobe S., Rietkerk F. (2017b) Breeding. In: Abelló M.T., Rietkerk F., Bemment N. (eds.) *EAZA Gorilla Best Practice Guidelines (*Gorilla gorilla gorilla). Barcelona, Spain: Barcelona Zoo, 84–107. https://www.eaza.net/assets/Uploads/CCC/2017-BPG-Gorilla-approved.pdf

Abramoff M.D., Magelhães P.J., Ram S.J. (2004) Image processing with ImageJ. *Journal of Biophotonics* 11(7): 36–42.

Ayaz M., Akand M., Kucukbagriacik Y., Dursunoglu D. (2015) The effects of estradiol on cardiac muscle electrophysiology in orchiectomized rat model: A new insight to side effects caused by castration. *European Review for Medical and Pharmacological Sciences* 19: 2866–2874.

Bailey S.E. (2004) A morphometric analysis of maxillary molar crowns of Middle-Late Pleistocene hominins. *Journal of Human Evolution* 47(3): 183–198. doi:10.1016/j.jhevol.2004.07.001

Bays H.E., Toth P.P., Kris-Etherton P.M., Abate N., Aronne L.J., Brown W.V., Gonzalez-Campoy J.M., Jones S.R., Kumar R., La Forge R., Samuel V.T. (2013) Obesity, adiposity, and dyslipidemia: A consensus statement from the National Lipid Association. *Journal of Clinical Lipidology* 7(4): 304–383. doi:10.1016/j.jacl.2013.04.001

EAZA (2019) Specialist Programmes. EAZA: European Association of Zoos and Aquaria. https://www.eaza.net/conservation/programmes/

Edney A.T., Smith P.M. (1986) Study of obesity in dogs visiting veterinary practices in the United Kingdom. *The Veterinary Record* 118(14): 391–396.

Galbany J., Martínez L.M., López-Amor H.M., Espurz V., Hiraldo O., Romero A., de Juan J., Pérez-Pérez A. (2005) Error rates in buccal-dental microwear quantification using scanning electron microscopy. *Scanning* 27(1): 23–29. doi:10.1002/sca.4950270105

Galbany J., Stoinski T.S., Abavandimwe D., Breuer T., Rutkowski W., Batista N.V., Ndagijimana F., McFarlin S.C. (2016) Validation of two independent photogrammetric techniques for determining body measurements of gorillas. *American Journal of Primatology* 78(4): 418–431. doi:10.1002/ajp.22511

Galbany J., Abavandimwe D., Vakiener M., Eckardt W., Mudakikwa A., Ndagijimana F., Stoinski T.S., McFarlin S.C. (2017) Body growth and life history in wild mountain gorillas (*Gorilla beringei beringei*) from Volcanoes National Park, Rwanda. *American Journal of Physical Anthropology* 163(3): 570–590. doi:10.1002/ajpa.23232

Gatti S., Levréro F., Ménard N., Gautier-Hion A. (2004) Population and group structure of western lowland gorillas (*Gorilla gorilla gorilla*) at Lokoué, Republic of Congo. *American Journal of Primatology* 63(3): 111–123. doi:10.1002/ajp.20045

Giraldo-Deck L.M., Goymann W., Safari I., Dawson D.A., Stocks M., Burke T., Lank D.B., Küpper C. (2020) Development of intraspecific size variation in black coucals, white-browed coucals and ruffs from hatching to fledging. *Journal of Avian Biology* 51(8): e02440. doi:10.1111/jav.02440

Hutchinson J.E., Fletcher A.W. (2010) Using behavior to determine immature life-stages in captives western gorillas. *American Journal of Primatology* 72(6): 492–501. doi:10.1002/ajp.20799

IUCN (2021) The IUCN Red List of Threatened Species. Version 2021-2. https://www.iucnredlist.org. [Accessed 8 November 2021]

Kessler M.J., Wang Q., Cerroni A.M., Grynpas M.D., Gonzalez Velez O.D., Rawlins R.G., Ethun K.F., Wimsatt J.H., Kensler T.B., Pritzker K.P.H. (2016) Long-term effects of castration on the skeleton of male rhesus monkeys (*Macaca mulatta*). *American Journal of Primatology* 78(1): 152–166. doi:10.1002/ajp.22399

Klailova M., Lee P.C. (2014) Wild western lowland gorillas signal selectively using odor. *PLoS ONE* 9(7): e99554. doi:10.1371/journal.pone.0099554

Koot S., Kapteijn C.M., Huiskes R.H., Kranendonk G. (2016) A note on the social compatibility of an all-male group of hamadryas baboons (*Papio hamadryas*). *Journal of Zoo and Aquarium Research* 4(1): 7–13. doi:10.19227/jzar.v4i1.105

Létang B., Rietkerk F., Szánthó J., Mulot B., Britton L., ter Meulen T., Guéry J.P., Sueur C. (2017) How does castration change integration of immature males in their familial group network in captive western lowland gorillas? *Folia Primatologica* 88: 177. doi:10.1159/000479094

Létang B., Mulot B., Alerte V., Bionda T., Britton L., ter Meulen T., Szánthó J., Guéry J.P., Sueur C. (2021) Social proximities of developing gorilla males (*Gorilla gorilla gorilla*) in European zoos: The consequences of castration and social composition. *Applied Animal Behaviour Science* 234: 105175. doi:10.1016/j.applanim.2020.105175

Licea M.E., Castelo L. (2006) Andropausia. *Revista Cubana de Endocrinología* 17(1). http://scielo.sld.cu/scielo.php?script=sci_arttext&pid=S1561-29532006000100007

Magliocca F., Querouil S., Gautier-Hion A. (1999) Population structure and group composition of western lowland gorillas in North-Western Republic of Congo. *American Journal of Primatology* 48(1): 1–14. doi:10.1002/(SICI)1098-2345(1999)48:1<1::AID-AJP1>3.0.CO;2-2.

Maklakov A.A., Lummaa V. (2013) Evolution of sex differences in lifespan and aging: Causes and constraints. *BioEssays* 35(8): 717–724. doi:10.1002/bies.201300021

McGreevy P.D., Thomson P.C., Pride C., Fawcett A., Grassi T., Jones B. (2005) Prevalence of obesity in dogs examined by Australian veterinary practices and the risk factors involved. *The Veterinary Record* 156(22): 695–702. doi:10.1136/vr.156.22.695

McKenzie B. (2010) Evaluating the benefits and risks of neutering dogs and cats. *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources*, 5: 1–18. d reproductive effort in male primates. *Hormones and Behavior* 91: 36–51.

Nieschlag E., Behre H.M. (1998) Pharmacology and clinical uses of testosterone. In: Nieschlag E., Behre H.M. (eds.). *Testosterone*. Berlin, Germany: Springer, 293–328. doi:10.1007/978-3-642-72185-4_10

Owens I.P.F., Short R.V. (1995) Hormonal basis of sexual dimorphism in birds: Implications for new theories of sexual selection. *Trends in Ecology and Evolution* 10(1): 44–47. doi:10.1016/S0169-5347(00)88967-3

Paniagua J.A. (2016) Nutrition, insulin resistance and dysfunctional adipose tissue determine the different components of metabolic syndrome. *World Journal of Diabetes* 7(19): 483–514. doi:10.4239/wjd.v7.i19.483

R Core Team (2019) R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Richards A.B., Morris R.W., Ward S., Schmitz S., Rothmond D.A., Noble P.L., Woodward R.A., Winslow J.T., Weickert C.S. (2009) Gonadectomy negatively impacts social behavior of adolescent male primates. *Hormones and Behavior* 56(1): 140–148.

Robbins M.M., Czekala N.M. (1997) A preliminary investigation of urinary testosterone and cortisol levels in wild male mountain gorillas. *American Journal of Primatology* 43(1): 51–64. doi:10.1002/(SICI)1098-2345(1997)43:1<51::AID-AJP4>3.0.CO;2-X

Rommerts F.F.G. (1998) Testosterone: An overview of biosynthesis, transport, metabolism and nongenomic actions. In: Nieschlag E., Behre H.M. (eds.) *Testosterone.* Berlin, Germany: Springer, 1–32.

Rose N.L., Yang H., Turner S.D., Simpson G.L. (2012) An assessment of the mechanisms for the transfer of lead and mercury from atmospherically contaminated organic soils to lake sediments with particular reference to Scotland, UK. *Geochimica et Cosmochimica Acta* 82: 113–135.

Sanborn L.J. (2007) Long-term Health Risks and Benefits Associated With Spay/Neuter in Dogs. http://www.naiaonline.org/pdfs/LongTermHealthEffectsOfSpayNeuterInDogs.pdf

Spain V.C., Scarlett J.M., Houpt K.A. (2004) Long-term risks and benefits of early-age gonadectomy in cats. *Journal of the American Veterinary Medical Association* 224(3): 372–379. doi:10.2460/javma.2004.224.372

Stubbs W.P., Bloomberg M.S., Scruggs S.L., Shille V.M., Lane T.J. (1996) Effects of prepubertal gonadectomy on physical and behavioral development in cats. *Journal of the American Veterinary Medical Association* 209(11): 1864–1871.

Sundburg C.R., Belanger J.M., Bannasch D.L., Famula T.R., Oberbauer A.M. (2016) Gonadectomy effects on the risk of immune disorders in the dog: A retrospective study. *BMC Veterinary Research* 12: 278. doi:10.1186/s12917-016-0911-5.

Takeshita R.S.C., Huffman M.A., Kinoshita K., Bercovitch F.B. (2017) Effect of castration on social behavior and hormones in male Japanese macaques (*Macaca fuscata*). *Physiology & Behavior* 181: 43–50. doi:10.1016/j.physbeh.2017.09.006

Vermeer J., Abelló M.T., Holtkötter M. (2014) Progress in the Western lowland gorilla *Gorilla gorilla gorilla* European Endangered Species Programme: A review of the decade 2002–2011. *International Zoo Yearbook* 48(1): 234–249. doi:10.1111/izy.12027

Wang Q., Kessler M.J., Kensler T.B., Dechow P.C. (2016) The mandibles of castrated male rhesus macaques (*Macaca mulatta*): The effects of orchidectomy on bone and teeth. *American Journal of Physical Anthropology* 159(1): 31–51. doi: 10.1002/ajpa.22833

Watts D.P. (1991) Mountain gorilla reproduction and sexual behavior. *American Journal of Primatology* 24(3–4): 211–225. doi:10.1002/ajp.1350240307

Wickham H. (2016) *ggplot2: Elegant Graphics for Data Analysis.* New York, New York: Springer-Verlag.

Yamagiwa J. (1986) Activity rhythm and the ranging of a solitary male mountain gorilla (*Gorilla gorilla beringei*). *Primates* 27: 273–282. doi:10.1007/BF02382071.

ZIMS (2014) Zoological Information Management System-Species360, Version 1.7 Updated: 27 January 2014. Available from https://zims.species360.org

Zuur A.F., Saveliev A.A., Ieno E.N. (2014) *A Beginner's Guide to Generalized Additive Mixed Models with R.* Newburgh, UK: Highland Statistics Ltd.